PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Volume 56, No. 1, pp. 1–22, 6 figs., 1 table (Appendix) April 29, 2005

Redescriptions of the Nudibranch Genera *Akiodoris* Bergh, 1879 and *Armodoris* Minichev, 1972 (Suborder Doridacea), with a New Species of *Akiodoris* and a New Family Akiodorididae

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The type species of the genus *Akiodoris, A. lutescens*, Bergh, 1880 is redescribed from specimens found in the Sea of Okhotsk, and from the Commander Islands, Russia. A second species in the genus, *Akiodoris salacia* Millen sp.nov., is described from the Pacific waters off British Columbia, Canada. The type species of the genus *Armodoris, A. antarctica* Minichev, 1972 from the Davis Sea, is redescribed from the type and two additional specimens. The relationship of these genera with other genera of phanerobranch dorids is explored and a new family Akiodorididae is formed for the suctorian genera *Akiodoris, Armodoris, Echinocorambe, Doridunculus*, and *Prodoridunculus*.

KEY WORDS: Opisthobranchia, *Akiodoris, Armodoris*, dorid phylogeny, Akiodorididae.

During the second half of 19th and early 20th centuries representatives of phanerobranch dorids of the genera *Akiodoris, Prodoridunculus* and *Doridunculus,* all with a remarkably similar radula, were discovered (G.O.Sars 1878; Bergh 1880; Odhner 1907; Thiele 1912). Bergh (1880) arranged the genus *Akiodoris* within the Suctoria, but *Doridunculus* was placed between the genera *Goniodoris* and *Ancula.* Following this arrangement, Fisher (1883–1887) placed the genus *Doridunculus* within the genus *Goniodoris* and the genus *Akiodoris (*as *Aciodoris)* within the genus *Acanthodoris,* in subgeneric ranks. Bergh (1883) created, for the first time, a phylogenetic scheme for the phanerobranch dorids where both genera *Akiodoris* and *Doridunculus* appeared at the base of Goniodorididae *sensu latu* as descendants of cryptobranch dorids. Later authors usually grouped the genera *Akiodoris, Prodoridunculus* and *Doridunculus* together into the base of the family Onchidorididae, probably considering them the most archaic forms (e.g., Thiele 1931; Odhner in Franc 1968), but Høisæter (1986) arranged *Doridunculus* near the genus *Lophodoris* in the family Goniodorididae. In the second part of last century Minichev (1972) added the genus *Armodoris* as closely allied to *Akiodoris.*

Millen (1987:19), in an abstract referring to a cladistic analysis of the family Onchidorididae, isolated the four genera mentioned above as a separate clade. Martynov (1997) suggested for these genera a new family, Akiodoridae, but he did not give a formal description for this taxon. The main goal of the present study is to revise the two principal genera, *Akiodoris* and *Armodoris,* and to explore their relationship with the families Goniodorididae and Onchidorididae.

The genus *Akiodoris* was erected by Bergh (1879 a) for a phanerobranch nudibranch which has tripinnate gills, a sessile buccal pump, smooth lip cuticle, two cuspidate lateral teeth per side, numerous rectangular marginal teeth, a penis armed with hooks and a vagina containing cilia covered villi. The type species, *Akiodoris lutescens* Bergh, 1880 was found in the Alaskan Aleutians, and this species has not been reported since. One of the authors, Alexander Martynov, found a large number of specimens in several museums and research institutions in Russia, all from the Commander Islands and from the Sea of Okhotsk, mainly in the Kuril Islands. Bergh's (1880) description was based on two specimens, one of which he considered a variety, although why he separated it is unclear. He never illustrated the external features and described them only briefly, although he described the anatomy in detail and included illustrations of some of the organs. A redescription of this species with emphasis on the morphology and additional illustrations of some of the anatomy is included in this paper. Martens (1879) emended the name to *Aciodoris*, replacing the Greek *Akio* (= sharp) with the Latin *Acio*. Because *doris* is a Greek name, we follow the recommendation of the Code that the components of a compound name should agree (Appendix D, II, 11) and revert to the spelling *Akiodoris*. *Aciodoris* is an unjustified emendation under the Code (art.32.5 and 33.2.3) and therefore a junor objective synonym of *Akiodoris*.

The other author, Sandra Millen, found 6 specimens of a small white dorid which possesses the internal characters of *Akiodoris*, in the waters near Vancouver, British Columbia, Canada. These animals differ in a number of external features from *Akiodoris lutescens* and represent a new species belonging to the genus *Akiodoris*. This species is described. and the relationship of the genus to other members of the family is discussed.

The genus *Armodoris* was created by Minichev (1972) for *A. antarctica* Minichev, 1972 from Tokarev Island in the Davis Sea. It has pear-shaped or conical, spiculose tubercles and a radula shape similar to that of *Akiodoris*, but with more teeth. There are up to six inner lateral teeth and up to eight outer lateral teeth per side. The specimen is 16 mm long and sexually mature; it is possibly a mature specimen of *Prodoridunculus gaussianus* as only very small specimens of *Prodoridunculus* have been found. Without having a size range of specimens to examine, we shall retain them as separate taxa. Minichev (1972) separated *Armodoris* from *Akiodoris* because in *Armodoris*, the gonad surrounds the stomach, he observed a single seminal bursa, the spermatheca, on a long duct, and the vagina did not have a villous lining. In our observations of *Akiodoris lutescens*, we found that the stomach is anteriorly buried and posteriorly exposed so that the gonad-covered digestive glands surround it. The spermatheca of *Akiodoris* is short stalked, but has a tubular shape similar to that of *Armodoris antarctica*. *Akiodoris salacia* sp. nov. lacks villi on the vagina. Thus, the taxonomical position of the genus *Armodoris* needs clarification. During a study of the collection of the Zoological Institute RAS (St. Petersburg), two addition specimens of *Armodoris antarctica* were found along with the dissected holotype of *A. antarctica*, which are used here for a redescription of this taxon.

Subclass Opisthobranchia
Order Nudibranchia
Suborder Doridacea
Superfamily Anadoridoidea

Family Akiodorididae Millen and Martynov, fam. nov.
TYPE GENUS: *Akiodoris* Bergh, 1879

Akiodorididae, nom. nudum: Martynov. 1997:233.

DIAGNOSIS. — The notum is spiculose, covered by rounded or elongate tubercles. Posterior part of the notum is round or transformed into two lobes. Branchial pocket is absent, gills are arranged in semicircle with the exception of aberrant *Echinocorambe* where they are reduced to one simple leaf. Head has small four-corned oral veil. Anus dorsal, except for *Echinocorambe* where it is ventral. Buccal pump is a diverticulum of the dorsal surface of the buccal bulb. Peripheral muscle is absent and there are small, separate muscles at the anterior part of buccal pump. Lip disk thin and smooth. Radular formula is 2-14.2-6. 0-1. 2-6. 2-14. Central tooth is usually present, ranging from a small plate to wide arch-shaped structure, sometimes with a central cusp. The first and following up to six lateral teeth have an irregular rectangular base and strong cusp directed downward and several strong denticles on one or both sides. Remaining laterals are in varying degrees of reduction, with a rectangular shape. Receptaculum seminis vaginal or inserted on the uterine duct. Stomach is entirely or partially free from the digestive gland. Prostate tubular or enlarged. Penis with or without spines.

The new family includes the following five genera: *Akiodoris* Bergh, 1879, *Armodoris* Minichev, 1972, *Doridunculus* G.O. Sars, 1878, *Echinocorambe* Valdés and Bouchet, 1998, and *Prodoridunculus* Thiele, 1912.

Genus *Akiodoris* Bergh, 1879

Type species *Akiodoris lutescens* Bergh, 1880, by monotypy

Diagnosis.— The notum is spiculose, covered by rounded tubercles. Posterior part of the notum is round and fully covers the foot and tail. Gills are in a semicircle. Head has a small four-corned oral veil. Anus dorsal. Buccal pump is slightly prominent anteriorly. Radular formula is 8-13.2.1.2.13-8. The central tooth is wide and arch-shaped. The first and second laterals have only 1–2 blunt denticles on both sides. Remaining laterals are in various degrees of reduction. Cerebral and pleural ganglia are fully fused. Stomach is very large and fully free from the digestive gland. Gonad does not cover most of the digestive gland and stomach. Prostate long, tubular. Vagina may have villi. Ejaculatory duct has simple or complex spines.

The genus contains only the type species and the new species described in this paper.

Redescription of *Akiodoris lutescens* Bergh, 1880

(Figs. 1–2)

Akiodoris lutescens Bergh, 1879a:354–355 (*nomen nudum*).
Akiodoris lutescens Bergh, 1879b:4–8 (plates only).
Akiodoris lutescens Bergh, 1880:55–58.

Material examined[3].— Holotype: The type specimen cannot be found in the University of Copenhagen Museum (Kathe Jensen, pers. commun.). Other Material: 1 specimen, 18 September 1949, Shikotan Island, Kuril Islands, Russia, 13.5 m depth, collected by E.F. Gurjanova. 1 specimen, 10 September, 1966, 44°41′N, 148°57′E, 780 m., Segsbee trawl, R/V "Vityaz," St. 5640. Collected by V.M. Koltun. 1 specimen, 31 July, 1971, Vasilieva Pt., Paramushir Is, Kuril Islands, Russia, 20 m depth, large stones, collected by P.G. Kraynyuk. 2 specimens, 5 August, 1970, Gilyak Pt., Paramushir Is, Kuril Islands, Russia, 20 m. depth, rock, collected by A.M. Murakhveri. 1 specimen, 10 August, 1970, Anciferova Is., Kuril Islands, Russia, 15 m depth, large stones, collected by A.M. Murakhveri. 1 specimen, 20 September, 1971, Gromky Pt., Iturup Is., Kuril Islands, Russia, collected by V.I. Lukin. 1 specimen, 20 September 1971, Gromky Pt., Iturup Is., Kuril Islands, Russia, 15 m depth, collected by V.I. Lukin. 1 specimen, 22 September 1971, Shutka Inlet, Iturup Is., Kuril Islands, Russia, 20 m depth, rock, collected by V.I. Lukin. 1 specimen, 14 July,

[3] Except as indicated, no specimen numbers are given inasmuch as most are in field station collections.

1972, Korabel'naya Inlet, 1 km to sw of Korabel'ny Pt., Medny Is., Commander Islands, Russia, 20 m depth, collected by V.I. Lukin. 2 specimens, 5 August, 1972, Kozyrevskogo Pt., Paramushir Is., Kuril Islands, Russia, 15 m depth, stones, collected by V.N. Romanov. 1 specimen (juvenile), 5 September 1973. Peregrebnogo Pt., Beringa Is., Kuril Islands, Russia, 20–22 m depth, collected by B.I. Sirenko. 2 specimens, 17 September, 1973. Cherny Pt., Medny Is., Commander Islands, Russia, 10 m depth, rock, collected by B.I. Sirenko. 1 specimen, 31 July, 1978 Iona Is., Okhotsk Sea, Russia, 80 m depth, big and small stones, collected by V.A. Pavlyuchkov. 4 specimens, 11 July, 1985, Lopatka Pt., Kamchatka Peninsula, Russia, 17 m depth, rock and stones, collected by V.I. Shalukhanov. 1 specimen, 10 July, 1985, Vladimira Pt., Atlasova Is., Kuril Islands, Russia, 25 m depth, rock. 1 specimen, ZMMU Lc-25738. 14 July, 1985, Sakhalinsky Bay, 54°57.5.N, 141°01.0.E, 95 m depth, R/V "G. Popov," dredge 5, collected by Yu. I. Kantor. 1 specimen, 4 August, 1985, Okhotsk Sea, 55°26′8″N, 145°55′3″W, 160 m depth, stones, collected by A.V. Smirnov. 1 specimen, 20 Aug. 1986, Gladkovsky Pt., Medny Is., Commander Islands, Russia, 10–12 m depth, rock, collected by V.V. Oshurkov. 1 specimen, 25 August, 1986 Monati Pt., Beringa Is., Commander Islands, Russia, 25 m depth, rock, collected by V.V. Oshurkov. 1 specimen, 22 July 1991, Podutesnaya Inlet, Beringa Is., Commander Islands, Russia, 20 m depth, rock, collected by V.I. Shalukhanov. 2 specimens, 14 August 1991, Buyan Pt., Beringa Is., Commander Islands, Russia, 10 m depth, rock, collected by V.I. Shalukhanov. 1 specimen, 23 July 1992, Sivuchy Kamen' Kekur Islet, Medny Is., Commander Islands, Russia, 20 m depth, rock, collected by K.E. Sanamyan. Specimens in Kamchatka's Institute of Ecology and Environment, Petropavlovsk-Kamchatsky, Russia, the Institute of Marine Biology, Vladivostok, Russia, the Zoological Institute, Saint Petersburg, and in the Zoological Museum, Moscow State University, Russia. 1 specimen, 11 July, 1985, Lopatka Pt., Kamchatka Peninsula, Russia, 17 m depth, rock and stones, collected by V.I. Shalukhanov.

External Morphology.— The body is elongate-oval and reaches a maximum preserved length of 40 mm (Fig. 1A). The dimensions of one specimen are $40 \times 25 \times 13$ mm. The mantle edge is 4–5 mm, barely covering the sides and tail in preserved animals, although the tail probably extends beyond the mantle in live animals. The notum is densely covered with differentially sized tubercles. The small tubercles, up to 0.4 mm in width, are conical or spindle shaped, the large tubercles, up to 1.4 mm in width, are rounded or cylindrical with round tips (Fig. 1B). Spicules lie in the notum radially around the tubercles, most of the spicules in the tubercles have been dissolved by formalin but traces remain, radiating loosely from the centre outward. The rhinophores have 10–15 lamellae and numerous spicules. The rhinophores contract into openings which do not have raised sheaths but are edged all around with 11–12 large tubercles. There are 10–17 tri- or quadripinnate gills which contract into depressions arranged in a broad horseshoe, which is broken posteriorly by a few tubercles. The gill size decreases towards the posterior, but sometimes a few small tripinnate gills are present anteriorly between the larger gills. Within the gill circlet are many large and some small tubercles, about 80 in total. The anal opening is not raised and is slightly left of centre towards the posterior end of the circlet.

The color in life, according to Dall, is light yellow (Bergh 1880). Preserved specimens are dirty white or pinkish-tan.

The head is veliform, not high, and slightly narrower than the foot. The mouth opening is round and the rounded tentacles are thicker on the anterior edge (Fig. 1C). The foot is broad and bilabiate anteriorly, posteriorly it extends into a small leaf-like tail, which is papillate on the dorsal surface.

Anatomy.— The oral tube is short and muscular. The anterior half of the buccal bulb has a poorly developed, sessile, rounded buccal pump (sucking crop) with no median muscular band

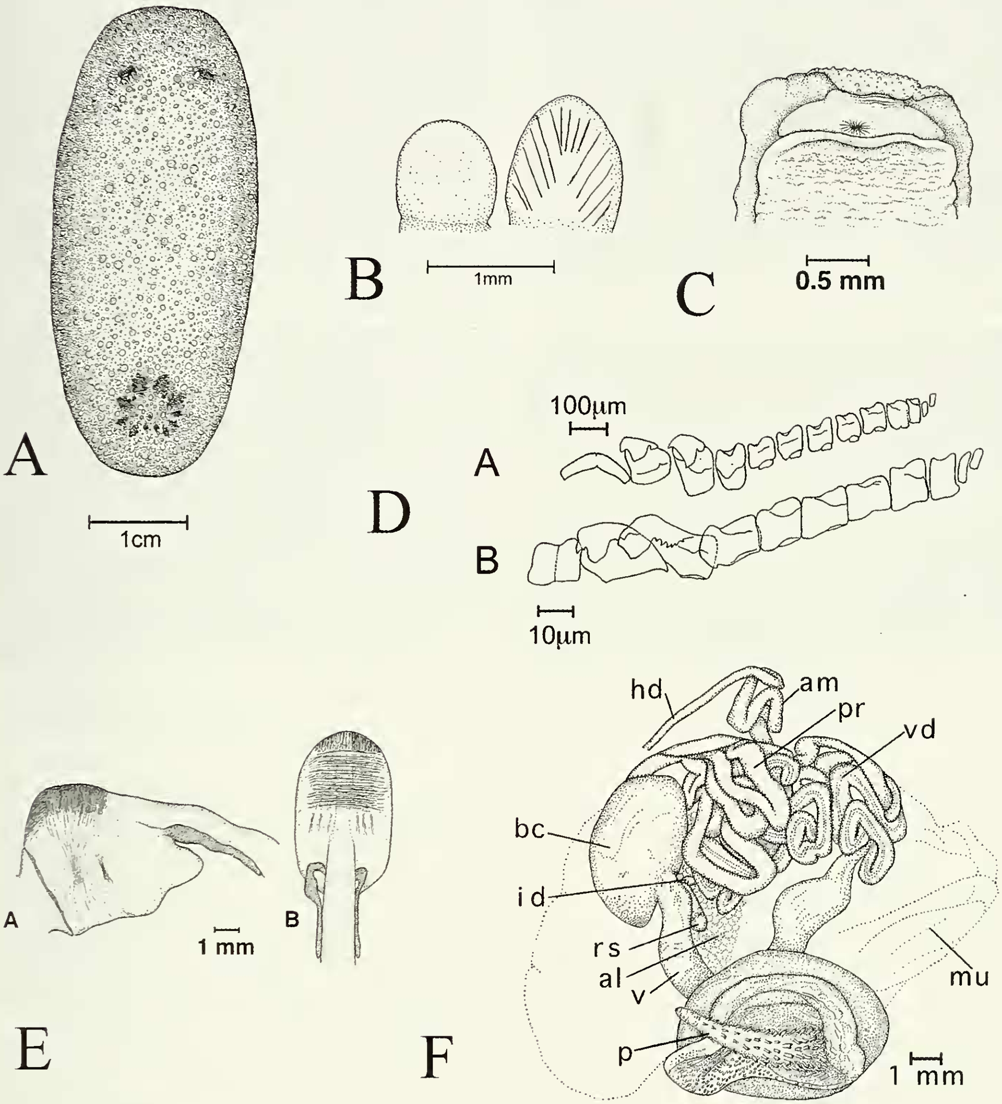


FIGURE 1. *Akiodoris lutescens*, drawn with a camera lucida. A. Whole animal, dorsal view. B. Tubercles, one showing traces of spicules. C. Head and anterior of foot. D. Radula, one half row and rachidian tooth. A. adult, B. juvenile. E. Buccal bulb, A. lateral view B. dorsal view. F. Reproductive system. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; hd, hermaphroditic duct; id, insemination duct; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd. muscular vas deferens.

(Figure 1E). The anterior part of the buccal pump has longitudinal muscular fibres, followed by a band of transverse fibres which extends down the sides of the buccal bulb. Posteriorly there are three longitudinal bands of muscles on each side of the esophagus. Ventrally there is a small posteriorly projecting radular sac. The round lip disk is muscular with a thick outer layer, smooth and yellowish in color. This outer layer is fleshy with only a thin cuticle coating. The radula has 52–69 rows of reddish brown teeth with the formula (8-13.2.1.2.13-8) (Figs. 1D, 2A–B). The central tooth

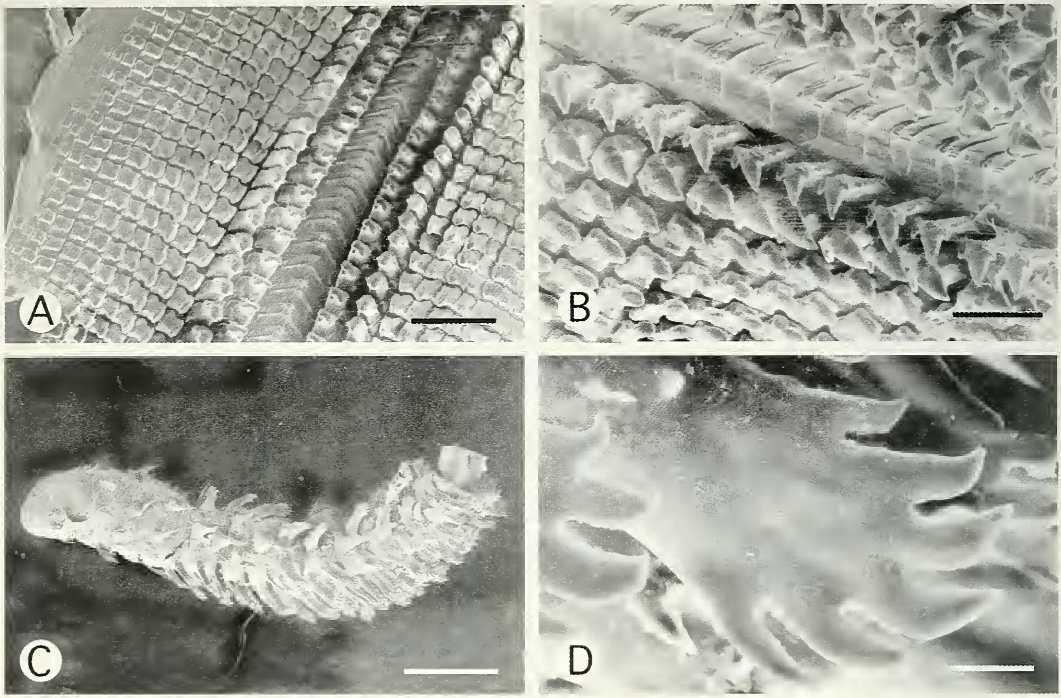


FIGURE 2. *Akiodoris lutescens*. Specimen from Lopatka Pt., tip of Kamchatka Peninsula, Russia, 11/7/85. A. SEM micrograph of radula, scale bar = 400 µm. B. SEM micrograph of central region of radula. Scale bar = 200 µm. C. SEM micrograph of entire penis. Scale bar = 1 mm. D. SEM micrograph of one posterior penial spine. Scale bar = 40 µm.

is wide and flat in the shape of a raised arch. Sometimes a small, posteriorly directed, chitinised denticle can be seen. The two lateral teeth per side can be seen in Fig. 2A–B. The first lateral teeth have a rectangular base and a short, wide, recurved cusp with one inner and one or two outer denticles. The second lateral teeth have a rectangular blade with a large quadrangular cusp on the inside and 5–6 outer denticles. The marginal teeth have rectangular bases and a small projection on the inner posterior corner. They diminish in size towards the outside, the last two being very small and narrow. The remainder of the digestive tract is as described by Bergh (1880), except that the ribbon shaped salivary glands are shorter, ending at the digestive gland.

The large blood glands are pinkish, not white, in color. The central nervous system is as described by Bergh (1880).

The reproductive system is shown in Figure 1F. Bergh (1880) described this system well although he only illustrated portions of it. The vagina is lined by villi, 0.6–0.8 mm long, with a dense axis and non glandular, ciliated epithelium. The penis in Bergh's specimen was retracted, the glans only partly everted. A fully everted penis is shown in Figure 2C and a closeup view of a posterior penial spine in Figure 2D. The reproductive openings are located on the right side about one third of the body's length from the anterior mantle edge. The surface around the genital openings is covered with numerous soft villi approximately 0.3 mm in length.

NATURAL HISTORY.— The known range is expanded from its original localities of Atka Island and Kyska Island in the Aleutians, westward and northward to the Commander Islands, southward along the Kamchatka peninsula and down the chain of Kuril Islands to Shikotan near Hokkaido and into the Sea of Okhotsk to Iona Island near its centre and Sakhalinskiy Bay in the west. It has been collected from low water line to depths of 780 m, usually between 10 and 25 m in the months of July, August and September. The only juvenile was collected in September. All specimens have been collected from rocky areas.

Akiodoris salacia Millen, sp. nov.
(Figs. 3–4)

Akiodoris sp. 1 Behrens, 1991:51, #68

ETYMOLOGY.— Named for the Roman sea-goddess Salacia, wife of Neptune.

MATERIAL.— HOLOTYPE: California Academy of Sciences, CASIZ 110807, 14 September 1985, Tyee Point, Copper Cove, British Columbia, Canada (49°22′8″N, 123°16′5″W), 20 m depth, on hydroids, rocky substrate, collected by S. Millen. PARATYPES: Royal British Columbia Provincial Museum, RBCPM 005-000013-001, 1 specimen, collected with the holotype. Zoological Museum of Moscow University, ZMMU, LC-25737, 1 specimen, collected with the holotype.

EXTERNAL MORPHOLOGY.— Preserved specimens of this small dorid range in length from 4 to 6.5 mm. The largest animal measures 6.5 × 3 × 2.5 mm (l × w × h). The body shape (Fig. 3A) is elongate-oval, wider in front than behind, with a slightly trailing tail. The mantle margin is fairly wide, covering the high sides and head but not the tail. Posteriorly, above the tail, the marginal edge is indented. The notum bears elongate, slightly inflated, spear shaped tubercles with pointed tips (Fig. 4A). There is little variation in tubercle size, which ranges from 0.08 to 0.4 mm in height and 0.06 to 0.18 mm in width. The numerous tubercles are spaced evenly over the notal surface, with a few small ones in the mid-dorsal area and some medium sized ones near the mantle edge.

Spicules are found in the lower ¾ of each tubercle, and their tips protrude slightly. The protruding spicules are rod-like, slimmer than those forming the central shaft inside each tubercle. At the bases of the tubercles, spicules extend in a radial, star-like pattern which can be seen through the notum. Within the notum there are scattered spicules forming a mesh-like network which forms a radial pattern towards the mantle margin. This pattern is only visible on the ventral surface of the mantle margin. There are scattered quadrate spicules stiffening the sides of the body.

In the foot, spicules form a mesh pattern on the sole, and the dorsal surface of the foot flange and the tail are heavily spiculated. Numerous sharp pointed spicules protrude in these areas, especially on the tail. The slightly raised margins of the rhinophores each bear 4–5 tubercles, the largest being the innermost anterior one. There are no tubercles within the branchial arch.

The rhinophores are sturdy and end in a rectangular, blunt tip. The stalk is short and most of the clavus bears wide, thick lamellae supported by spicules. The 8–10 lamellae are attached along a vertical, anterior line which appears inset due to the sudden indentation of the wider lamellae. The lamellae slope ventrally and become narrower towards the posterior where they meet forming a chevron.

The 4–6 contractile gills are bipinnate and incompletely tripinnate, non-retractable, separated on the outside, but joined at their bases towards the inside. They are arranged in a semi-circle which is open posteriorly. The gills are largest anteriorly and directed towards the posterior. The gills are surrounded by tubercles, but none are within the small semicircle. The anus is at the posterior end of the gill arch.

Living specimens (Fig. 3A) are white or faintly yellow in color. There are sometimes a few opaque white specks in the dorsum along the sides and in front of the rhinophores. In immature animals the central area appears pinkish due to the underlying color of the reddish-brown digestive gland. In more mature animals, the digestive gland is covered by creamy-yellow gonads giving the central area a peach hue. Ventrally the digestive gland shows only faintly through the foot. The

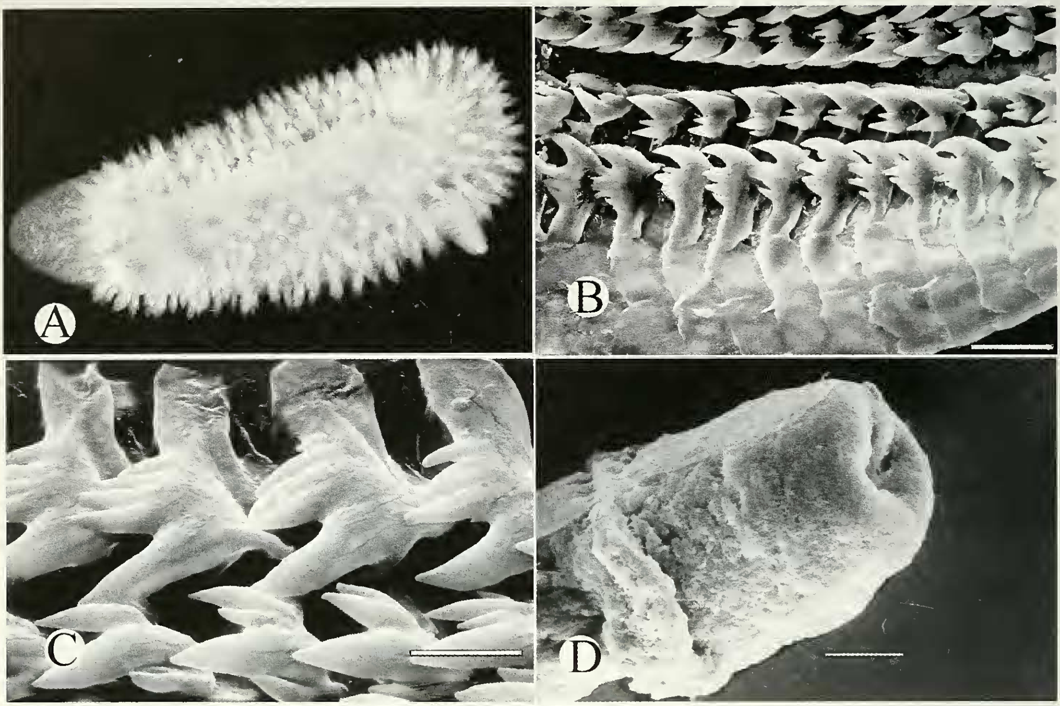


FIGURE 3. *Akiodoris salacia* sp. nov. Specimen from Tyee Pt., near Vancouver, British Columbia, Canada, 14/9/85. A. Photograph of a live specimen of *A. salacia*, 4.6 mm in length. B. SEM micrograph of the radula. Scale bar = 20 µm. C. SEM micrograph of the lateral teeth. Scale bar = 10 µm. D. SEM micrograph of the penis. Scale bar = 40 µm.

anterior edge of the foot and the head are sometimes pale yellow. The rhinophores are pale yellow and the gills are pale yellow or white. An unusual feature of this species is a series of opaque white, round, granular glands along the overhanging posterior border of the mantle. There are 8–10 of these glands, the smallest being located on the midline.

The head (Fig. 4B) is composed of two triangular lobes which end in flap-like tentacles separated from the rest of the head by a dorsal groove. The foot is narrow and elongate, wider and truncate anteriorly. The anterior edge is bilabiate. The triangular tail protrudes up to 0.5 mm. It is thick but does not have a dorsal keel. Noteworthy are its many, posteriorly projecting spicules.

ANATOMY.— The oral tube is a muscular ring with short labial glands surrounding it. The buccal bulb (Fig. 4C) has a dorsal, rounded, sucking crop which is sessile, with no median muscular band and weak peripheral muscles. The radular sac is short and protrudes from a wide, muscular odontophore. The round lip disk is thinly cuticularized and smooth.

The radula has 35–39 tooth rows. The radula formula is 3-5.2.1.2.5-3 (Figs. 3B–C, 4D). There is no well-developed rachidian tooth but the central area has a thickened, raised plate which begins at the fourth or fifth tooth row. The plate is 3–6 µm long. The innermost lateral tooth has a rectangular base and a large, recurved, pointed cusp. It has one inner and two or three outer, well developed denticles. These laterals range in width from 12.5–24 µm and 13–19 µm in length. The outer lateral teeth have a rectangular base with a large, recurved hook on the inside and three or four well developed outer denticles. The outer laterals are 18–19 µm wide and 12–18 µm long. Each marginal tooth is a flat, rectangular plate with slightly rounded outer corners and a small spine on the inner posterior corner. The marginal teeth diminish in width towards the outside. The marginal

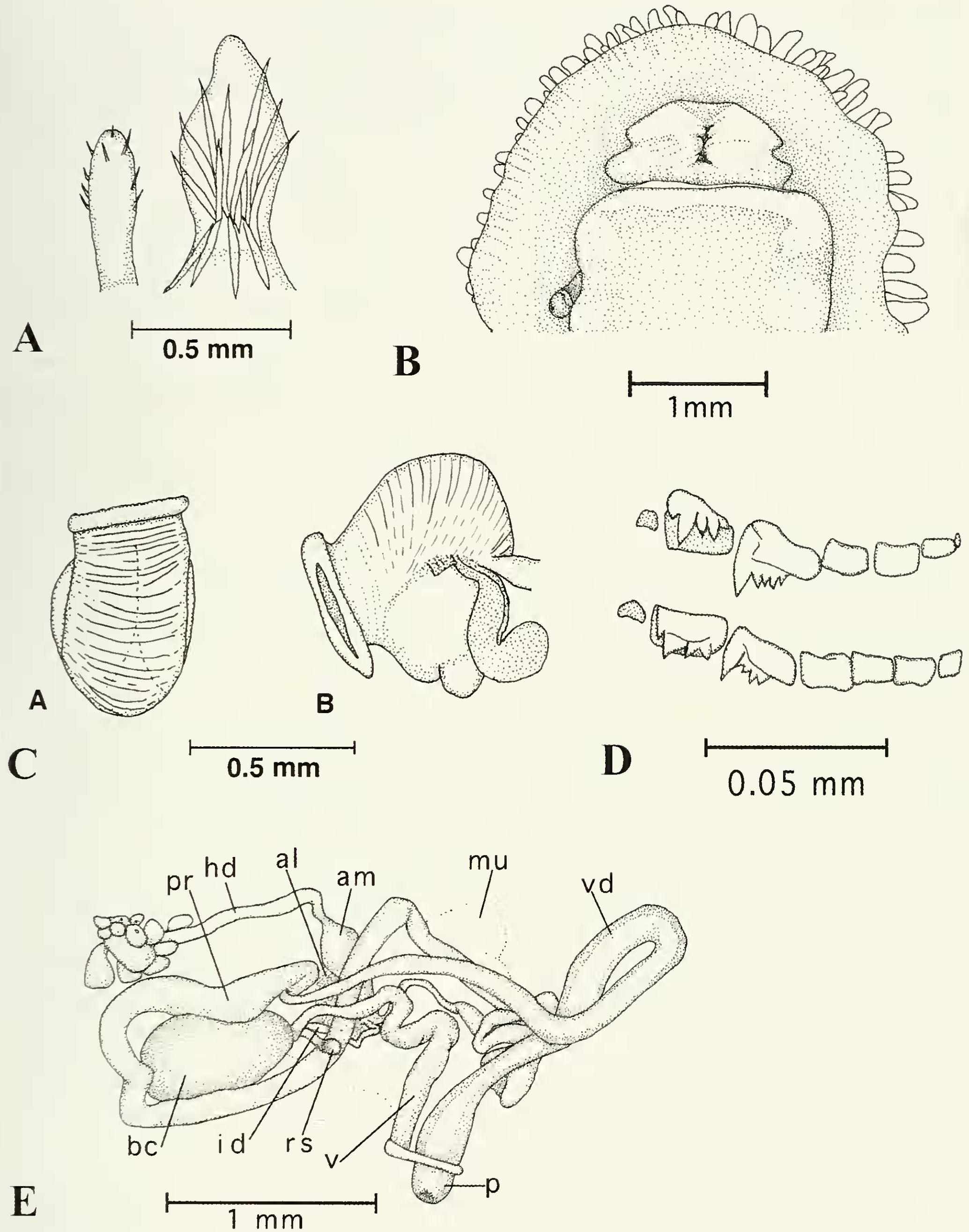


FIGURE 4. *Akiodoris salacia*, drawn with a camera lucida. A. Tubercles, one showing internal spicules. B. Head and anterior of foot. C. Buccal bulb. A. dorsal view, B lateral view. D. Radula. One half row including rachidian plate. E. Reproductive system. Key: al, albumen gland; am, ampulla; bc, bursa copulatrix; hd, hermaphroditic duct; id, insemination duct; mu, mucous gland; p, penis; pr, prostate; rs, receptaculum seminis; v, vagina; vd, muscular vas deferens.

teeth range in width from 6–19 µm and in length from 6–10 µm.

The salivary glands are small, flattened, elongate-oval masses lying under the buccal bulb and attaching to it at the anterior end of the esophagus (Fig. 4C). The esophagus is a narrow tube which becomes slightly wider and softer before entering the digestive glands. The digestive glands appear as one elongate mass, wider in front than behind and truncated on the anterior right side. The stomach is sac-shaped, almost entirely separated from the digestive glands. It has a small, round caecum on the right border of the anterior part of the stomach, tucked in the loop of the intestine. The intestine is broad and runs to the right of the midline curving inward to the anus. The anal opening is not raised.

The pericardial sac contains a posterior, thin-walled, triangular auricle and a smaller, more muscular, diamond shaped ventricle. The flattened, compact blood glands are located just posterior to the central nervous system.

The fused cerebro-pleurals are oval and joined by a short commissure. The olfactory nerves have bulbous bases with small attachment points. The large, black eyes have very short stalks. The oval pedal ganglia, smaller than the cerebro-pleurals, are located directly below them and are connected to them by a short commissure. They are connected together by a commissure which is slightly longer than the cerebral one. The small oval, paired buccal ganglia adjoin each other.

The reproductive system is illustrated in Figure 4E. It lies on the right side with the loop of the vas deferens extending from the region of the mouth to a short distance in front of the gills. The ovotestis consists of oval, creamy-yellow lobules lying on the dorsal and lateral surfaces of the digestive glands. The branched gonoducts are broad bands which unite to form one central pre-ampullar duct. This duct widens slightly into a tubular ampulla. There is a short post-ampullar duct which bifurcates into an oviduct and a long vas deferens. A short distance from its origin, the vas deferens becomes prostatic, loops posteriorly towards the ovotestis, encircles the bursa copulatrix and continues anteriorly. It then becomes non-prostatic, loops back on itself and bends downward. The long, tubular, non-prostatic portion enlarges slightly to form a penal bulb containing the uncoiled vas deferens. The penis joins a common atrium with the vagina. It is a cylindrical papilla. Inside, the distal portion of the vas deferens is weakly chitinised and has small spines, 5–8 µm in length. The penis (Fig. 3D) is eversible, but the spines were not everted on any of the specimens.

The vagina is long and cylindrical, wider near its opening posterior to the penis in the common atrium, and gradually narrowing. It loops back on itself and then gives off a short duct to the large, round bursa copulatrix. The insemination duct, after a short distance, is joined by a short duct from the tubular receptaculum seminis. The insemination duct is long and winding. It terminates at the oviduct near its junction with the post ampullary duct and entrance to the female gland mass.

The female gland mass has an oval, yellow albumen gland. The hermaphroditic ampulla runs down its anterior surface.Surrounding it, anteriorly, posteriorly, and on the inner side is a white mucous gland. The separate oviductal opening is ventral to the common genital atrium. The two reproductive openings are located high on the right side about ⅓ of the body's length from the anterior mantle edge.

Natural History.— The specimens described in this paper were found in September at a depth of 20 m. on a rocky bottom swept by moderate currents. They were all found on an old hydroid colony intermingled with the ctenostome bryozoan *Farrella elongata*, which is presumed to be their food. The larger specimens had partially mature reproductive systems and were copulating, but no spawn was present or laid in the laboratory during the week subsequent to their capture.

Remarks.— The newly described species is placed in the genus *Akiodoris* Bergh, 1879 because it has a nearly identical reproductive system, bi- and tripinnate gills, smooth lip disk, sessile pharyngeal bulb, stomach which is free from the digestive glands, digestive caecum, and armed penis. However, in the presence of a slight posterior mantle reduction and gills arranged in a small, non-tuberculose semi-circle with a posterior anus, *A. salacia* is more similar to the genus *Doridunculus*. We considered this similarity as superficial due to the small size of *A. salacia* and relative frequency of appearance of a pair of lobe-like structures in the posterior part of the notum in phanerobranch dorids, apparently caused by partially delayed ontogenetic processes in notum formation.

There are a number of differences between *Akiodoris lutescens* and *A. salacia*. Externally, the tubercles differ in that *A. salacia* has long, similar sized, lanceolate tubercles with projecting spicules, whereas *A.lutescens* has smaller, conical and rounded tubercles of varying sizes. In *A. salacia*, the gill opening is in a small semi-circle with no enclosed tubercles and the anus is at the posterior edge. In *A.lutescens*, the gill pocket forms a large horseshoe enclosing many tubercles and the anus. The posterior mantle margin is slightly indented in the new species, but this does not appear to be the case in *A. lutescens*. Both species have a flat leaf like tail which is dorsally spiculated. The distinctive mantle glands of *A. salacia* can only be seen in live specimens, so their presence cannot be used as a distinguishing feature. Only preserved *Akidoris lutescens* have been observed. Internally, the radula has fewer (4–5) marginal teeth than a similar sized (6 mm) juvenile *A. lutescens*, which had 7–9 marginal teeth (Fig.1D). The thickened cuticular central tooth observed in specimens of *A. salacia*, is not well developed, but it may develop in older specimens. Only in larger *A. lutescens* does the central cuticle form a chitinised spine on the rachidian tooth. The central nervous system of the two species varies in that the eyes are large and sessile in *A. salacia* and smaller and on long stalks in *A. lutescens* and the unusual lateral position of the pedal ganglia found in *A. lutescens* was not found in *A. salacia*.

Genus *Armodoris* Minichev, 1972

TYPE SPECIES *Armodoris antarctica* Minichev, 1972, by monotypy

DIAGNOSIS.— The notum is spiculose, with rounded tubercles. Posterior part of the notum is round and fully covers the tail. Gills are in a semicircle. Head has a small four-corned oral veil. Anus dorsal. Buccal pump is oval and prominent. Radular formula is (4-8.4-6.1.4-6.4-8). The central tooth is a square plate of moderate size with a slightly prominent central cusp. The lateral teeth have a rectangular base and one long cusp to the inside of center. Denticles are found on the first 6 teeth, the outer 4–8 have one reduced cusp or are reduced to rectangular bases. Cerebral and pleural ganglia are fully separated. Only a small dorsal part of the stomach is free from the digestive gland. Gonad covers most of the digestive gland and stomach. Prostate massive. Interior of vagina is simple. Ejaculatory duct has simple spines.

The genus contains only the type species.

Redescription of *Armodoris antarctica* Minichev, 1972

(Figs. 5–6)

Armodoris antarctica Minichev, 1972:366–368, fig 4; Cattaneo-Vietti et. al., 2000:175.

TYPE MATERIAL.— HOLOTYPE: ZIN N 1[4] (dissected, most internal organs are removed and are

[4] ZIN — The Zoological Institute, Russian Academy of Sciences, St. Petersburg; the numbers refer to systematic catalogue, without inventory numbers in this case.

[5] There are no exact data in the first description of *Armodoris antarctica*, nor on the label that accompanies the holotype, except for Minichev's personal label "19-2". The present date, depth and substrata is reconstructed by comparison with neighboring labels "19-1" and "19-3", which both have complete or semi-complete data.

not traceable, radula slide not found), around January 19, 1966[5], 11th Soviet Antarctic Expedition, Davis Sea, Tokarev Id., Between Samples 45 and 55, Depth about 30–32 m, rock, collected by A. F. Pushkin. OTHER MATERIAL: 2 specimens (ZIN N 2[4], N 3[4]), Zoological Institute, Russian Academy of Sciences, February 1, 1969, 13th Soviet Antarctic Expedition South Shetland Ids., King-George Id., La Guardia Nacional Bay, transect I, St. XXI, sample 60, 36 m depth, stones, collected by A. F. Pushkin.

EXTERNAL MORPHOLOGY.— Preserved specimens range in length from 13 to 16 mm. The holotype measures 16 × 9 × 5 mm (l × w × h) (Fig. 5 A–C). The specimen, ZIN N 3, is 13 × 7.4 (l × w). The body shape is elongate-oval, slightly wider in front than behind. The mantle margin is amply wide, fully covering the sides and tail. Posteriorly, the marginal edge is without any traces of an indent. The notum bears tubercles of different sizes, scattered small tubercles between the larger ones. In the middle of notum, longitudinally, there are some rather large, pear-shaped tubercles. They become more elongate or cylindrical toward to the notal margins. Tubercles sizes range from 0.07 to 1 mm in height and 0.06–0.7 mm in diameter. Spicules within a tubercle are rod-like, varying in size, nearly straight or slightly crooked. The spicules sometimes slightly extruded through upper part of the tubercle. The margins of the rhinophore pockets are very low and bear 6 blunt tubercles (right side of the specimen ZIN N 3) and 4 in the holotype. The rhinophores have about 10 lamellae.

Six (ZIN N 3) to nine (holotype) contractile, but non-retractile, gills are unipinnate and incompletely bipinnate (Fig. 5D). They are arranged in a semi-circle, which is posteriorly completed by a large tubercle. The gills are surrounded by elongate tubercles. The holotype and ZIN N 2 specimen have three tubercles inside the gill semicircle, whereas example ZIN N 3 has none. The anus is in front of the posterior tubercle in the 13-mm length specimen. Preserved specimens are whitish-pinkish or yellowish.

The head is a small semi-oval oral veil with two short blunt lobes extending posterio-laterally (Fig. 6C) The foot is rather wide, anteriorly truncated without any traces of post oral lobes. Posteriorly, the foot narrows slightly to form a flat, blunt tail (Fig. 6C).

ANATOMY.— The oral tube is short and muscular. Almost the entire upper part of the buccal bulb has a well-developed, oval buccal pump (Fig. 6E). The buccal pump has no peripheral muscle (median muscular band). The anterior part of the buccal pump has longitudinal muscular fibers, followed by a band of transverse fibers, which extends down the sides of the buccal bulb. The round lip disk is smooth, covered by a colourless cuticle. Radular formula is 36–52 (4-8.4-6.1.4-6.4-8) (Fig. 6D). The central tooth is a thin square plate of moderate size with a slightly prominent central cusp. The inner laterals are denticulate, and they gradually transform to the simple small plates of the outermost laterals. The first and at least 4–5 following laterals have a rectangular base and short or moderately long cusp (cusp of 2nd and 3rd laterals, in general, stronger than first ones) directed downward, usually straight or slightly curved. The first three or four inner laterals have 1–3 denticles on both sides of the cusp, the following 3–5 laterals have a serration (or it is reduced) on the outer side of the cusp. The remaining two to four laterals have a greatly reduced cusp, devoid of denticles, and the outermost tooth is just a simple plate. The elongate-oval salivary glands are small and attach to the buccal bulb at the anterior end of the esophagus (Fig. 6E). The latter is a rather wide, flattened tube. The stomach is sac-shaped, only a small dorsal portion is separate from the digestive gland (Fig. 6B). There is no caecum on the stomach.

The pericardial sac contains a posterior, thin walled narrow-triangular auricle and smaller, oval shaped ventricle (Fig. 6B). The blood glands are slightly visible and located posterior to the central nervous system.

The cerebral and pleural ganglia (Fig. 6B, 6F) are separated and the later are smaller. The

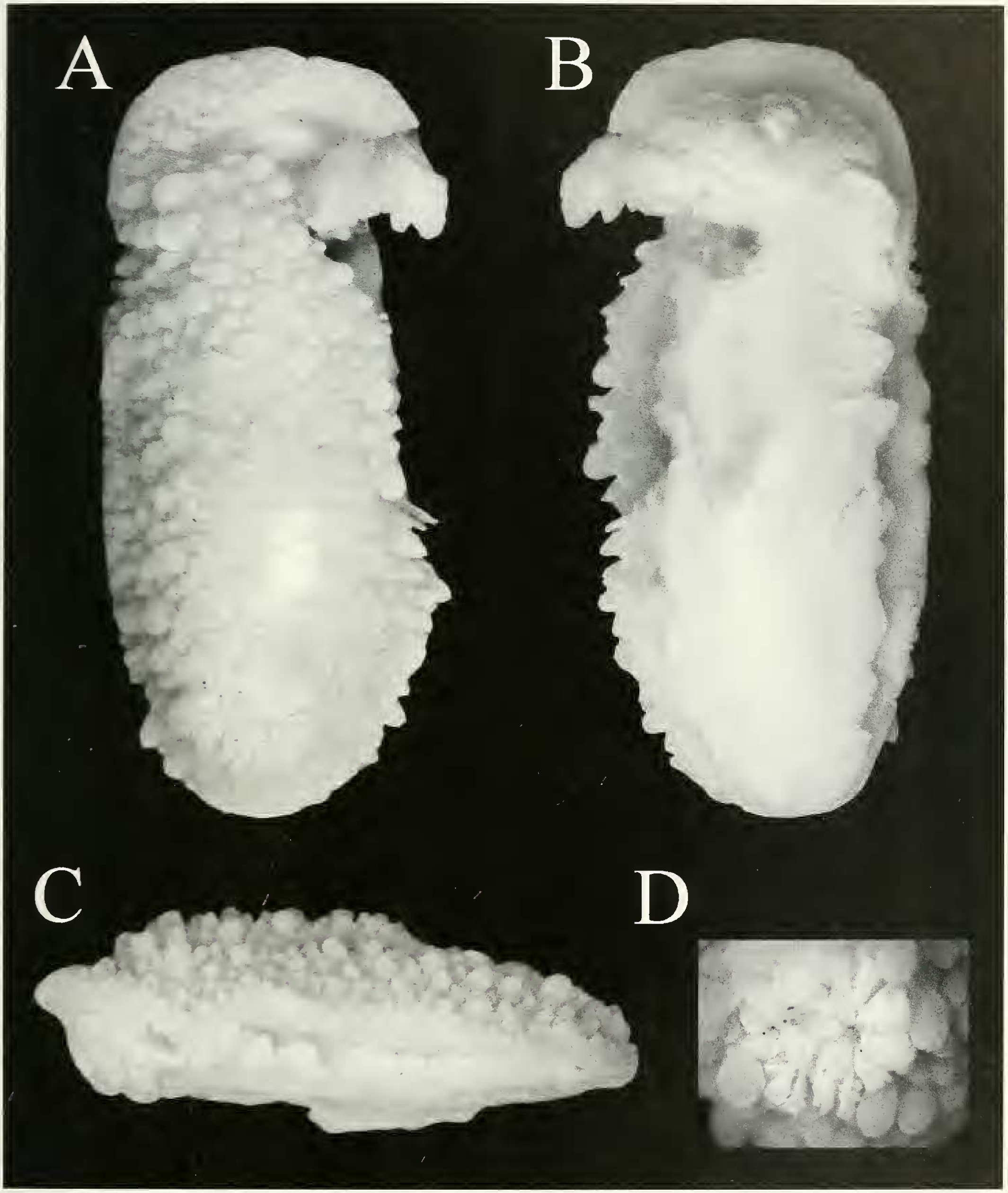
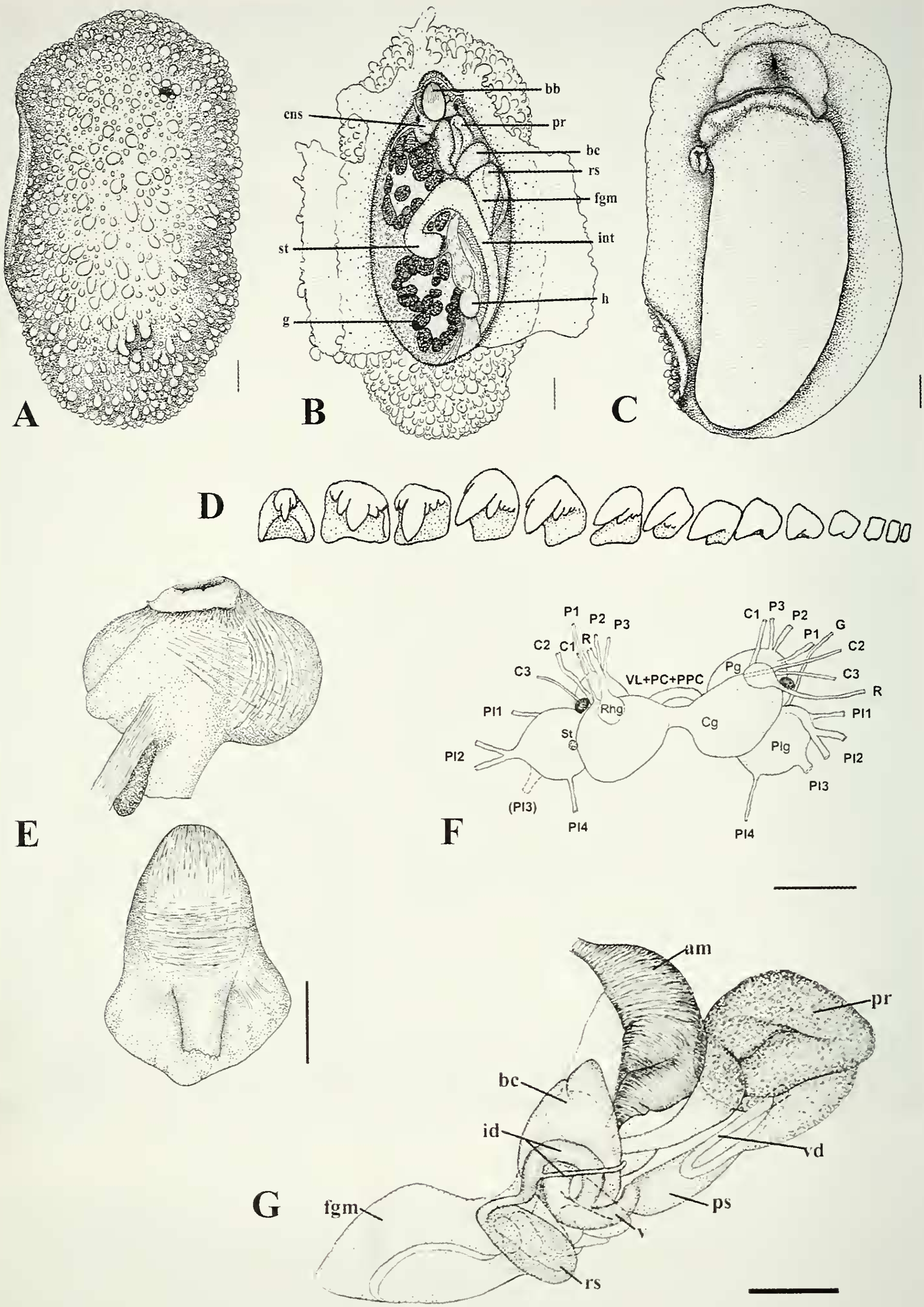


FIGURE 5. *Armodoris antarctica*, holotype. A. dorsal view. B. Ventral view. C. lateral view. D. Close up of the gills and tubercles.

large, black eyes have very short stalks. The pedal ganglia, similar in size to the cerebral, lie below them and are connected to them by short commissures. The rhinophoral ganglia are roundish. The buccal ganglia are roundish-oval. Gastro-esophageal ganglia were not found. In the cerebrals, three pairs of cerebral nerves were detected, in the pleurals, four, and in the pedals, three.

The ovotestis is characterised by large female follicles (Fig. 6B). The ampulla is voluminous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and kidney-shaped (Fig. 6G). There is a short post-ampullar duct, which bifurcates into an oviduct and a long vas deferens. The pre-prostatic duct is relatively long and wide. The prostatic part of vas deferens is a very massive tangle of a few thick, flattened loops. The prostate doesn't encircle the bursa copulatrix. The vas deferens narrows rapidly to a non-prostatic portion, loops back on itself, and bends downward. The deferent duct is a thin, muscular, not very long, gradually enlarging duct, which widens to an elongate penial bulb. The penial bulb joins a common atrium with the vagina. The ejaculatory duct of vas deferens has inside tiny, densely placed, spines. A partially everted penis is very narrow. The vagina is rather short and wide, similar in diameter its whole length, bending in the middle and entering the large, irregularly-triangular, bursa copulatrix. Villi inside the vagina are absent. The receptaculum seminis is oval and has a long, muscular, gradually widening duct, which joins the middle of the insemination duct. In the holotype, the receptaculum seminis is more elongate. The insemination duct is long, leaving the vagina near the middle and entering the female gland mass near the oviduct.

REMARKS.— The genus *Armodoris* has at least four to six well developed inside lateral teeth and no clear border between inner and outer laterals, whereas the genera *Akiodoris*, *Prodoridunculus* and *Doridunculus* have two well-differentiated inner laterals and rest of the laterals demonstrate reduction. *Echinocorambe* has three inner laterals, markedly different from the outer teeth. The radulas of *A. lutescens* and *A. salacia* are similar in the shape of the two first laterals and in the reduction of most of the outer laterals. This is a parallel case with the genus *Adalaria,* where the first lateral is more or less stable, but outer laterals have tended to reduce. The stomachs of *Akiodoris* and *Doridunculus* are massive and mostly free from the digestive gland, whereas *Armodoris* has a rather small free part of the stomach. *Armodoris* has large female follicles, which may be due to direct embryonic development, but the stomach is not fully surrounded by the gonad, as erroneously reported by Minichev (1972). The ampulla of *Armodoris* is large, more like that of *Doridunculus echinulatus*. Both *Akiodoris* species have similar long, but tubular prostates, whereas the prostate of *Armodoris* is massive. The receptaculum seminis is very narrow and tube-shaped in both *Akiodoris* and *Doridunculus*, but in the King-George's examples of *Armodoris* it is oval and in the holotype it is narrow-oval. The villi of the vaginal duct are not present in *Armodoris*. The buccal pump in *Armodoris antarctica* is more developed, although it has the same structure as found in *Akiodoris*, *Doridunculus* and *Echinocorambe*. Due to above differences between *Armodoris* and the other four genera with similar radular teeth, it is suggested that we maintain the genus *Armodoris*.

Compared to the King George Island examples, the dissected holotype has well preserved gills and oral veil. Minichev (1972) incorrectly interpreted the reproductive system and partially the digestive system of *A. antarctica*. He found only one receptaculum ("spermatheca" in his terms) and although he noted that "a 'spermatocyst' (= bursa copulatrix) is not evident in the present material", nevertheless, he considered this case to be a "unique feature" (Minichev 1972:366). The holotype originated from the Davis Sea, and the two additional specimens originated from another corner of Antarctic, the South Shetland Islands. An additional specimen of *A. antarctica* is the "Italian

FIGURE 6. *Armodoris antarctica* drawn with a camera lucida. A. Dorsal view, scale bar = 1 mm. B. Dissected view, scale bar = 1 mm. Key: bb, buccal bulb; bc, bursa copulatrix; cns, central nervous system; fgm, female gland mass; g, gonad; h, heart; int, intestine; pr, prostate; rs, receptaculum seminis; st, stomach. C. Ventral view, scale bar = 1 mm. D. Radula. One half row including rachidian tooth. E. Buccal bulb, Dorsal and lateral views. Scale bar = 0.5 mm. F. Central nervous system. Scale bar = 0.5 mm. Key: C 1-3, cerebral nerves; Cg, cerebral ganglia; P 1-3, pedal nerves; PC, pedal connective; PPC, pleuro-pedal connective; Pg, pedal ganglia; Pl 1-4, pleural nerves; Plg, pleural ganglia; R, rhinophoral nerve; Rhg, rhinophore ganglia; St, Statocyst; VL, visceral loop. G. Reproductive system. Scale bar= 1 mm. Key: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; id, insemination duct; ps, penis sheath; pr, prostate; rs, receptaculum seminis; v, vagina; vd, muscular vas deferens.

sample" from the stomach of a fish, *Trematomus bernacchii*, caught in the Ross Sea, Terra Nova Bay (Cattaneo-Vietti 2000). By the courtesy of Stefano Schiaparelli, we have studied a SEM image of the radula of the Italian specimen of *A. antarctica*. The radulas of all four specimens of *A. antarctica* are similar. The rarity of *Armodoris antarctica* is caused by its inhabiting only shallow waters on rocky substrates, and it can only be found by diving collections, which is certainly rare in the Antarctic, especially around 30 m (both holotype and two additional samples were collected slightly below 30 m on rocky substrates and in remote localities).

Phylogenetic Analysis

Dorid nudibranchs are currently divided into two groups, those with gills and rhinophores which retract into a closable pocket, the Eudoridoidea (=Cryptobranchia), and those whose gills and rhinophores have no pocket or an open pocket, the Anadoridoidea (= Phanerobranchia). The phanerobrachs dorids were in turn subdivided by Bergh (1892) into two groups, those with a suctorial buccal apparatus (suctorians) and those without (non-suctorians). These are informal groups, but the three families that Bergh placed into the suctorians, Corambidae, Goniodorididae, and Onchidorididae, are commonly arranged together. There have been numerous rearrangements within these three families over the years, but currently the family Onchidorididae is believed to contain the genera *Acanthodoris, Adalaria, Akiodoris, Arctadalaria, Armodoris, Calycidoris, Diaphorodoris, Doridunculus, Onchidoris* and *Prodoridunculus*, although Wägele and Willan (2000) consider the genera *Akiodoris* and *Armodoris* to belong to the Goniodorididae following Bergh (1883), who placed them at the base of the Goniodorididae.

Four of these genera form a distinct clade based primarily on their radular characteristics (Millen 1987). Most genera in the family Onchidoridae have on each side a single, large, strongly hooked lateral with a triangular base and narrow, hooked, marginal teeth. The rachidian, where present, has an elongate, rectangular shape. In contrast, a clade of four genera, *Akiodoris, Armodoris, Doridunculus,* and *Prodoridunculus*, have two or three (sometimes up to 6), wide, rectangular lateral teeth per side. The first lateral has internal and external denticles, the second and third, when present, have external denticles. The rachidian tooth, if present, is arch-shaped. The marginal teeth are wide and rectangular with a small hook. These four genera also have a relatively simple buccal pump.

Recent cladograms using either molecular or morphological data, which have included a variety of cryptobranch and phanerobranch dorids, have suggested that the phanerobranch dorids may, in fact, be polyphyletic (Wollscheid and Wägele 1999; Wägele and Willan 2000; Wollscheid-Lengeling et al. 2001; Vallès et al. 2001; Váldes 2002). These studies have not shown suctorian dorids to be polyphyletic, nor have they been able to use the full range of genera in the family Onchidoridae. The genera used were those with hook-shaped teeth, *Acanthodoris, Adalaria, Calycidoris, Diaphorodoris*, and *Onchidoris*, which generally clustered together. To observe the characters which distinguish *Akiodoris* and *Armodoris* from other genera and to establish their closest relationships, and to which family they should be assigned, we produced a cladogram using all of the possible Onchidorididae genera. These were compared to sister taxa consisting of three genera from the Corambidae (*Corambe*, Loy and Echinocorambe) and one Goniodorididae (*Goniodoris*). One cryptobranch dorid, family Chromodorididae (*Cadlina*), was used as a sister taxa to the phanerobranchs. The outgroup and basal rooting was based on the basal Anthobranchiate dorid genus *Bathydoris*, using *B. spiralis* Valdés, 2002, which is closest to the cryptobranch and phanerobranch dorids (*fide* Valdés 2002). In total, 15 taxa and 29 characters were analysed using MacClade and PAUP 3.1.1.

The 29 characters used in this analysis are listed below: 23 characters are binary and 6 are multistate. Character states are indicated by numbers; 0 is the plesiomorphic condition and 1–2 are apomorphic. Non-applicable and unknown characters are coded with a ?. Polarities are the result of outgroup comparison. Table 1 (see Appendix) shows the distribution of plesiomorphic and apomorphic states.

1. *Mantle rim*: The mantle rim (projecting edge) is narrow, partially absent in *Bathydoris* and some phanerobranch dorids (0) whereas it covers the sides and foot in most dorids (1).

2. *Posterior mantle rim*: The posterior mantle rim, where distinct, is usually entire in *Bathydoris* and most dorids (0). It is bilobed in some phanerobranch dorids (1).

3. *Tail*: The tail is extended in *Bathydoris* and some phanerobranch dorids (0). It is small and covered by the mantle in most dorids (1).

4. *Ridge on tail*: The tail is usually smooth in *Bathydoris*, cryptobranch dorids and most phanerobranch dorids (0). It has a mid-dorsal crest or ridge in some phanerobranch dorids (1).

5. *Notal spicules*: Some *Bathydoris* and most dorid nudibranchs have integumentary spicules in the notum (0). These are absent in a few dorid species (1).

6. *Notal sculpture*: Sculpture in the form of deciduous villi is present in *Bathydoris* (0); most species of dorid nudibranchs have well attached tubercles (1). Only a few species are smooth (2).

7. *Head*: The head in *Bathydoris* and most phanerobrach dorids is veliform (0). Cryptobranch dorids have a round head and separate tentacles (1).

8. *Rhinophore sheath*: *Bathydoris* and some phanerobranch dorids have rhinophores which lack sheaths and are attached directly to the dorsum (0). Other phanerobranch dorids have non-contractile sheaths into which the rhinophores can retract (1). Cryptobranch dorids have contractile rhinophore sheaths which close over retracted rhinophores (2).

9. *Rhinophores*: *Bathydoris* and most other dorids have lamellate rhinophores (0). A few dorids have smooth rhinophores (1) which may have vertical envelopes (2).

10. *Gill protection*: *Bathydoris* and some phanerobranch dorids have gills which lack sheaths and are inserted directly on the notum (0). Some phanerobranch dorids have sheaths into which the gills can retract but which do not close over the gills (1). Cryptobranch dorids have contractile gill sheaths which close over the retracted gills (2). For taxa with no mantle gills, this character has been treated as non-applicable.

11. *Gill number*: *Bathydoris* and most dorids have more than five gills (0). A few species of phanerobranch dorids have less than five gills which is considered a reduction (1).

12. *Gill location*: *Bathydoris* and most dorids have the gills located on the mantle some distance from the edge (0). Some phanerobranch dorids have the gills posterior at the mantle edge or below it (1).

13. *Notal sculpture within the gill circlet*: *Bathydoris* and cryptobranch dorids do not have papillae or tubercles within the area encircled by the gills (0). Some phanerobranch dorids have notal sculpture in this area (1). For taxa with no mantle gills, this character has been treated as non-applicable.

14. *Anus location*: *Bathydoris* and most dorids have the anus located on the mantle some distance from the edge (0). Some phanerobranch dorids have the anus posterior at the mantle edge or below it (1).

15. *Lip disk*: *Bathydoris* has thick chitinous labial armature and other dorids may have various rods or papillae to strengthen the lip disk (0); a smooth, thin cuticle is considered apomorphic (1).

16. *Buccal pump*: A sucking pump on the pharynx is absent in *Bathydoris*, non-suctorian

phanerobranch dorids and cryptobranch dorids (0). This pump distinguishes the suctorian phanerobranch dorids (1).

17. *Peripheral muscles*: A median longitudinal band of muscles is not found on the phanynx of *Bathydoris* and most dorids (0). This muscle is found on some of the suctorian phanerobranch dorids (1).

18. *Rachidian tooth*: A rachidian tooth is present in *Bathydoris* and some dorids (0). Many dorids have lost this central tooth (1).

19. *Number of teeth per half row*: Primitive dorids and *Bathydoris* have many teeth, >10, per half row (0). Reduction has resulted in narrower radulas with fewer than 10 lateral teeth (1).

20. *Number of inner laterals*: Inner lateral teeth tend to be more highly developed than the outer lateral (marginal) teeth which are often reduced. In *Bathydoris*, and some dorids, only the first lateral tooth differs from the outer lateral teeth (0). In other dorids there are 2 or more teeth which can be differentiated from the outer laterals (1).

21. *Shape of innermost lateral tooth*: *Bathydoris*, some cryptobranch and some phanerobranch dorids have cuspidate innermost lateral teeth. The cusp is towards the center of a broad tooth and denticles may appear on one or both sides (0). Other, phanerobranch dorids have beak-like teeth, with a long cusp on the outer edge, and denticles, when present, only on the inner side (1).

22. *Denticulation on innermost lateral tooth*: *Bathydoris* has denticulations on both sides of the inner lateral teeth, as do some dorids (0). Other dorids, used here, may have denticulations only on the inner side (1) or they may be absent (2).

23. *Marginal teeth or outer lateral teeth*: In *Bathydoris* and many cryptobranch dorids, these are elongate, hamate teeth, with or without denticles on the outer side (0). In some phanerobranch dorids they are reduced to either an elongate-oval plate (1) or a wide, rectangular plate (2).

24. *Ampulla*: The hermaphroditic ampulla is narrow and undifferentiated in *Bathydoris* and many dorids (0). It is wide and usually short in some dorids (1).

25. *Penial spines*: Spines on the eversible vas deferens of the penis are absent in *Bathydoris* and some dorids (0). Small spines are present in a number of dorids and their presence is considered an apomorphy (1).

26. *Seminal receptacle*: This sac for sperm storage is absent in most *Bathydoris* species, but present in *Bathydoris spiralis* as a small sac with one duct (stalked) (0). In some dorids, it has two ducts (unstalked), which is considered derived (1).

27. *Seminal receptacle insertion*: This sac is inserted by its duct on the vagina in *Bathydoris spiralis* and many other dorids (0). In some dorids, it is inserted part way along the insemination (uterine) duct (1).

28. *Oviduct*: The oviduct carrying the eggs usually passes directly into the female gland mass (0). In a few dorids, it enters the seminal receptacle before entering the female gland mass, which is considered apomorphic (1).

29. *Cerebro-pleural ganglia*: These ganglia are separate in *Bathydoris* and a few dorids (0). They are fused in most dorids (1).

Phylogenetic Results

The data matrix results in one tree (Fig. 7), 64 steps long, with a consistency index of 0.562 and a retention index of 0.692. The Bremmer support index values (values to the right of the line in Fig. 7) show that most of the branches are poorly supported, with the exception of the clade containing those phanerobranch dorids with beak-shaped laterals (value 2) and the node containing Corambe and Loy (value 2+).

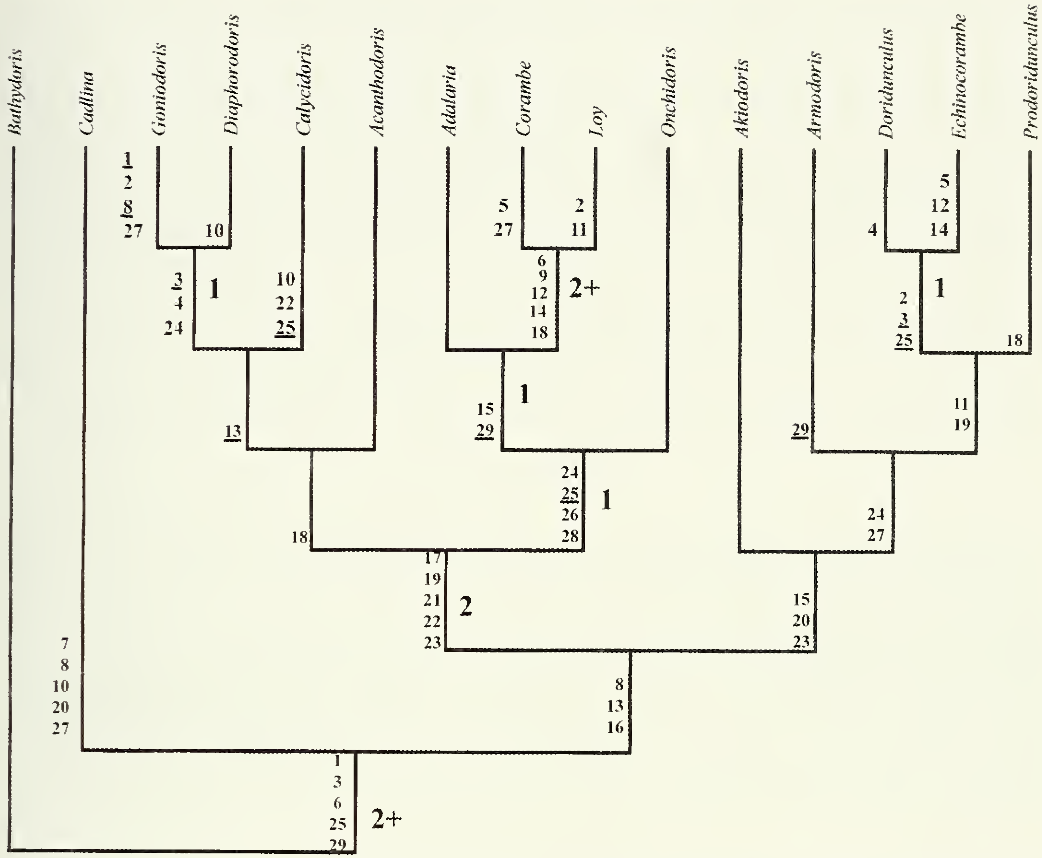

Figure 7. Strict consensus tree of a preliminary phylogeny. Apomorphies are indicated by character numbers included in the analysis. Characters which exhibit reversal are underlined. Bremer support values are 0 unless indicated by large numerals on the right side of the nodes.

In the resulting tree, the cryptobranch dorid *Cadlina* separates as a sister group to the remaning suctorian phanerobranch dorids, which are supported by the synapomorphies of non-contractile rhinophore sheaths (#8), the presence of papillae within the gill circlet (#13) and the presence of a buccal pump (#16).

These suctorian phanerobranch dorids traditionally belong to three families, Corambidae, Goniodorididae and Onchidorididae, but some members of the three families clustered together into one clade. This clade is distinguished by the presence of a peripherial muscle in the buccal pump (#17), a reduced half row of the radula (#19), one inner lateral tooth (#22), beak-shaped inner laterals (#21), and elongate oval outer laterals (#23). The Corambidae nests within the Onchidorididae and the genus *Goniodoris* nests with other members of the Onchidorididae and next to *Diaphorodoris*. Already the Superfamily Onchidoridoidea Gray, 1827 has been used to combine family Corambidae and Onchidorididae by Valdés and Bouchet (1998). Our data suggest that the families Corambidae and Onchidorididae are closely related (see Martynov 1994) and should be combined into one family, as suggested by Martynov (1999); the family group name Onchidorididae Gray, 1827 has priority. Further study is needed to clarify the position of *Goniodoris* and other members of the Goniodorididae in relation to this family.

The second clade contains members of the 'basal' Onchidorididae, which have sometimes been placed into the Goniodorididae. In this clade are the genera studied in this paper, *Akiodoris* and *Armodoris*, together with the closely related *Doridunculus* and the poorly known *Prodoridunculus*. Another poorly known genus, *Echinocorambe*, initially was placed in the family Corambidae by Valdés and Bouchet (1998) inasmuch as it has similar paedomorphic features. It was also suggested by Martynov (2000) that it is close to *Doridunculus* because of its similar radula and buccal pump; it may, in fact, be a juvenile of the latter. The cladogram confirms that it belongs in the same clade as *Doridunculus*. These five genera are in a clade with similar radulas, buccal pumps, and reproductive systems. Synapomorphies which distinguish this clade are the presence of a smooth, thin, lip disk (#15), two or more inner lateral teeth (#20), and the possession of rectangular, reduced outer laterals (#23). The distant position of *Goniodoris* in relation to this clade suggests that these five genera should not be in the family Goniodorididae. This clade forms a sister group to the clade containing the Onchidorididae (including Corambidae) and *Goniodoris*. Thus, this clade is considered a distinct family, Akidorididae Millen and Martynov, fam. nov.

Acknowledgments

We thank Dr. Tanya Korshunova (Moscow, IHNA and NF RAS) for drawings and photographs of *Armodoris antarctica*. We are also thankful to Dr. Alexi Chernyshev for figures used in plate 1 and additional sketches of *Akiodoris lutescens*. Ron Long, Simon Fraser University, kindly supplied the photograph of *Akiodoris salacia*. Stefano Schiaparelli provided an SEM image of the radula of *A. antarctica*. We also thank Sven Donaldson and John McNickol for diving assistance. This research was partly funded by the Department of Zoology, University of British Columbia to Sandra Millen. Partial funding to Alexander Martynov was from the Russian Federal Program "Study of Antarctic biota, Project N 16." Funding for publication costs is from the National Science Foundation, PEET Program (DEB-9978155) to Dr. Terrence Gosliner.

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Appendix

TABLE 1. Data matrix showing the distribution of character states (see text for details).

	1	2	3	3	5	6	3	8	9	19	16	12	18	19	15	16	17	18	19	21	21	22	24	24	25	21	27	28	29
Bathydoris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cadlina	1	0	1	0	0	1	1	2	0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1
Goniodoris	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	●	1	0	1	1	1	1	1	0	1	0	1
Acanthodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	●	1	0	1	1	1	0	1	0	0	0	1
Adalaria	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	1	0	1	0
Akiodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	2	0	1	0	0	0	1
Armodoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	0	2	1	1	0	1	0	0
Calycidoris	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	1	1	●	1	0	1	2	1	0	0	0	0	0	1
Corambe	1	●/1	1	0	1	2	0	1	1/2	?	0	1	?	1	1	1	1	●	1	0	1	1	1	1	0	1	1	1	0
Diaphorodoris	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	1	●	1	0	1	1	1	1	1	0	0	0	1
Doridunculus	1	1	0	1	0	1	0	1	0	0	1	0	0/1	0	1	1	0	0/1	1	1	0	0	2	1	0	0	1	0	1
Onchidoris	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	1	0	1	0	1	1
Prodoridunculus	1	0	1	?	0	1	?	1	?	?	1	?	?	?	?	?	?	1	1	1	0	0	2	?	?	?	?	?	?
Echinocorambe	1	1	0	0	1	1	0	1	0	?	1	1	?	1	?	1	0	0	1	1	0	0	2	?	0	?	?	?	?
Loy	1	1	1	0	0	2	0	1	1	?	1	1	?	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0